

**Takasi YAMAZAKI*: The embryology of *Shortia uniflora*
with a brief review of the systematic
position of the Diapensiaceae**

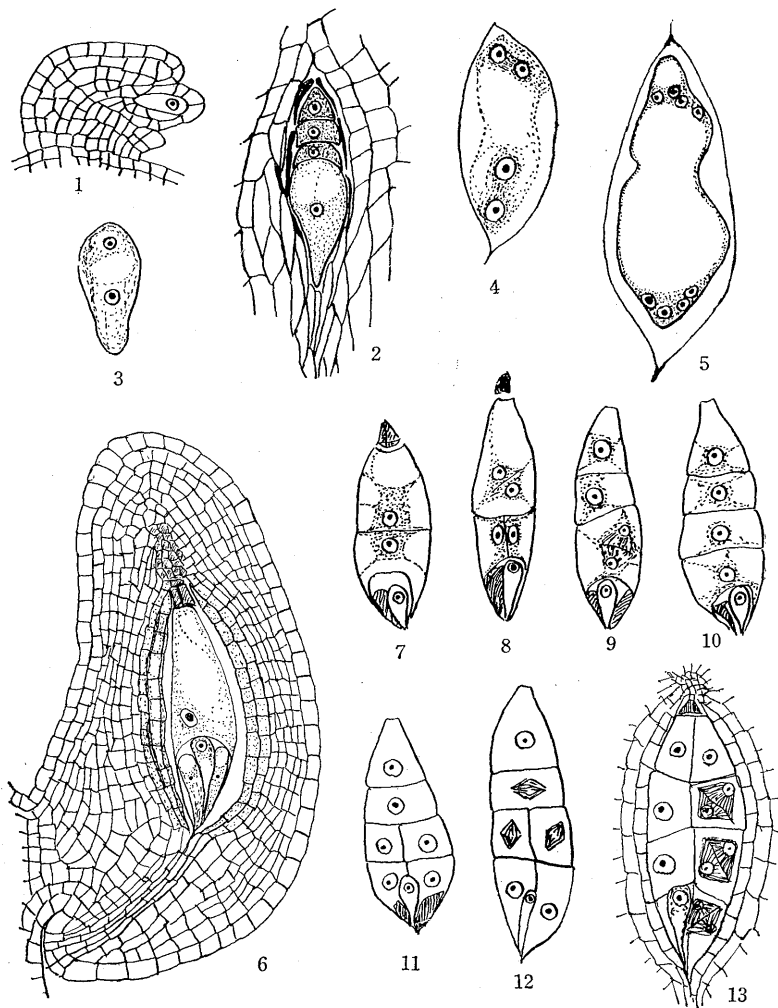
山崎 敬*: イフウチワの胚発生とイフウメ科の類縁

The material was mostly collected from Izugatake, Nishitama-gun, Tokyo pref., and fixed in formalin-acetic-alcohol. The sections were cut at the thickness of 10-15 microns and stained Heidenhain's iron-haematoxylin.

Ovule and embryo sac. The ovary is trilocular, as common as in other members of Diapensiaceae and has axial placentation with many anatropous ovules. The mature ovule has a single integument of 8-10 cell layers in thickness. The integumental cells of the chalazal part form the thick walled hypostatical tissue (fig. 6). A single hypodermal archesporial cell differentiates in the young nucellus (fig. 1). The archesporial cell functions as the megaspore mother cell and divides transversely to form a linear tetrad of four megaspores (fig. 2). The cell of chalazal end functions and gives rise to the embryo sac. This undergoes three successive divisions resulting in the formation of 2-, 4- and 8-nucleate gametophytes (figs. 3-5). The nucellus that is represented by a single layer of cells degenerates so early, that at their 2- or 4-nucleate stage, the gametophyte itself becomes to be directly surrounded by the integument. At the 8-nucleate gametophyte stage, the inner epidermal cells of the integument usually contain more cytoplasm than the other integumentary cells, but do not constitute the definite endothelium. The mature embryo sac is fusiform in shape. The micropylar region of the embryo sac contains two synergids and an egg cell. The chalazal region is occupied by three small antipodal cells in which the two cells lie side by side and the other single cell occupies the chalazal end. The antipodals start to disintegrate in early endosperm formation. The polar nuclei come to lie very near in the middle part of the embryo sac.

Formation of the endosperm. The endosperm is of the cellular type. The first division of the primary endosperm nucleus takes place with a transverse wall to form a micropylar and a chalazal chambers (figs. 7-8). The second division in the chalazal cell is transverse, but sometimes oblique, while the micropylar cell divides irregularly, in one case, first longitudinally and second transversely, in

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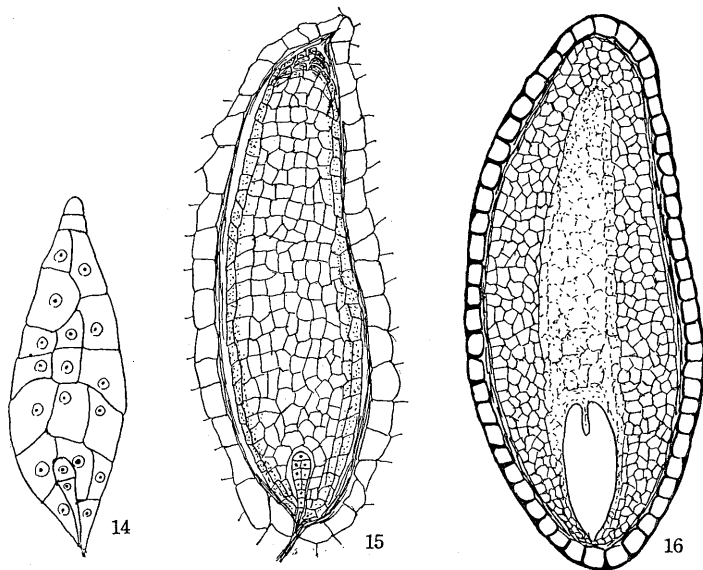


Figs. 1-13. *Shortia uniflora*. Stages in development of the embryo sac and endosperm.
 1. $\times 200$, 2-4. $\times 400$, 5. $\times 270$, 6. $\times 200$, 7-13. $\times 170$.

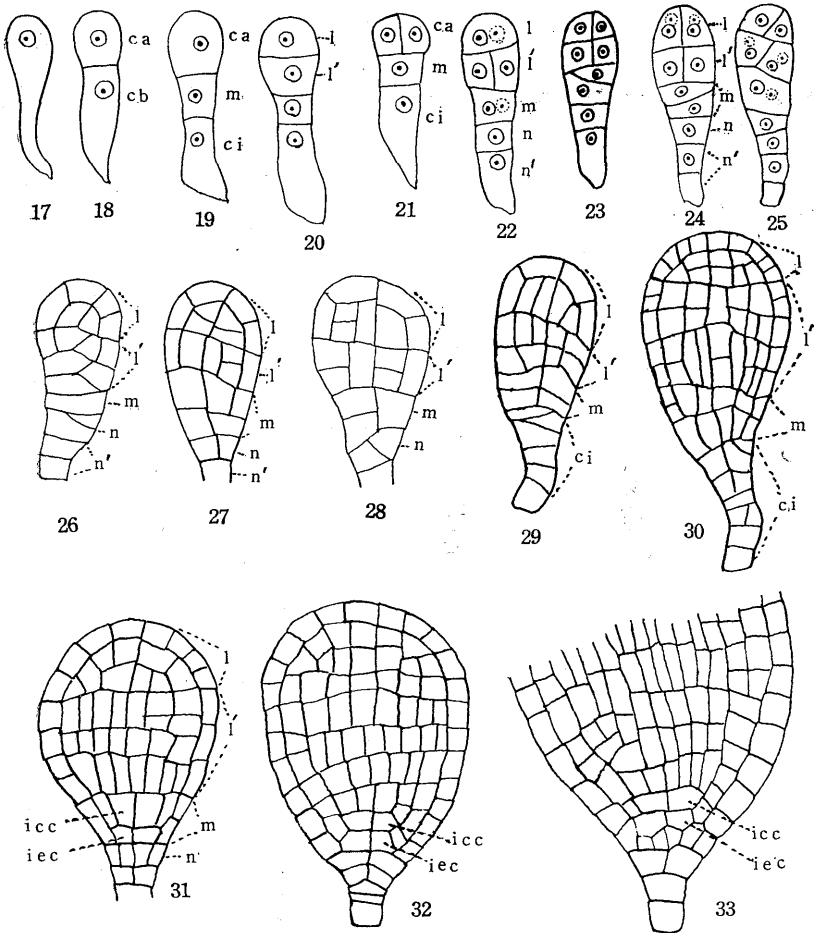
another case, in the reverse order (figs. 9-12). In spite of the above mentioned facts, in the second division the endosperm has a tendency to be arranged in a linear tier of four cells. Subsequent divisions are irregular (figs. 13-15). All the cells divide and contribute to the endosperm formation. The mature endosperm is ellipsoidal body consisted of many cells. The endosperm haustorium cannot be

found anywhere (fig. 16).

Embryogeny. After the fertilization, the zygote elongates considerably (fig. 17). Most of the cytoplasm remains near the tip of the elongated zygote cell and the nucleus is also located in this position. The first division is transverse resulting in an apical *ca* and a basal cell *cb* (fig. 18). The upper cell *ca* divides transversely to form the tiers *l* and *l'* (fig. 20), but rarely divides longitudinally (fig. 21). The tier *l* and *l'* later divide by vertical walls oriented at right angles (rarely at the same direction) to each other to give rise to four cells (figs. 22-23). Longitudinal divisions at right angles to the new walls in each tiers result two tiers of four cells each (figs. 24-25). Four cells of the upper tier *l* are divided by tangential wall to form outer and inner daughter cells (fig. 26). The outer daughter cells are divided only by anticlinal wall and give rise to the epidermal initials. The divisional sequence of the inner daughter cells is not definite, whether longitudinal followed by transverse, or in the reverse order (figs. 27-29). Inner daughter cells thus formed of the tier *l* differentiate to be the mother cells of the cotyledonary initials exteriorly and the elements which constitute the stem apex interiorly (figs. 30-32). Four cells of the lower tier *l'* are divided by longitudinal walls to produce eight



Figs. 14-16. *Shortia uniflora*. Stages in development of the endosperm and seed coat. 14. $\times 150$, 15. $\times 85$, 16. $\times 60$.



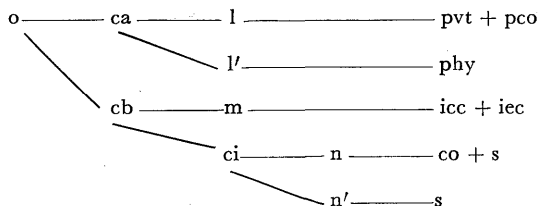
Figs. 17-33. *Shortia uniflora*. Stages in the embryo formation. $\times 300$.

cells. The resultant outer daughter cells of the tier *l'* repeatedly divide anticlinally and give rise to the epidermal initials, and the inner cells by continuous periclinal and anticlinal divisions form the plerome and periblem initials (figs. 30-32).

The basal cell *cb* divides transversely to form the tiers *m* and *ci* (fig. 19). The tier *m* is redivided comparatively slowly to form the initials of the central cylinder of the stem *icc*, and the initials of the central cylinder of the root *iec*. The tier *ci* divides transversely to form two cells, *n* and *n'* (fig. 22). The upper cell *n*

differentiates as the initial of the central part of the root cap *co*. The lower cell *n'* undergoes a few transverse divisions and contributes to the formation of the suspensor *s*.

The processe of the embryo fromation of *Shortia uniflora* is schematized as follows:



Seed coat. At the mature embryo sac stage, the integument consists of 8-10 layers of parenchymatous cells. The growth and expansion of the endosperm is accompanied by progressive digestion of the integument except the outermost layer of them. In the late development of the seed coat, the epidermal cells of the integument enlarge greatly and are filled with a highly stainable materials.

Discussions. Diapensiaceae has often been included in the order Ericales (Diels 1914, Hutchinson 1959), or has been placed in an independent order Diapensiales near the Ericales (Schultze-Motel 1964, Palser 1963). In *Shortia uniflora*, the ovules are unitegumic, and the nucellus is single layered which disappears during the megaspore development. In addition to these, the inner layer of the integument constitute an endotheliaceous tissue. All these characters agree very well with those of the typical Ericales.

In the typical Ericales (Ericaceae, Pyrolaceae, Epacridaceae and Empetraceae; Samuelsson 1913, Copeland 1933, Palser 1951, Stevens 1911 and Doyle 1941), the first and second divisions of the primary endosperm cell is regularly transverse resulting in a linear tier of four cells. In the Diapensiaceae the first endosperm division is mostly transverse, but the second division of the micropylar cell is tending to be frequently irregular. In *Diapensia lapponica* and *Galax aphylla* (Palser 1951) the division of the micropylar cell is frequently longitudinal, while in *Shortia galacifolia* (Palser 1951) the second division is most frequently longitudinal in both calazal and micropylar cells. In *Shortia uniflora* the division of the micropylar cell is frequently transverse and only rarely longitudinal, so that the endosperm has commonly be arranged in a linear tier of four cells. In the typical Ericales, the endosperm forms the micropylar and chalazal haustoria, but in the Diapensiaceae

these are absent. These characters along with the irregularity of the division of micropylar cell of the Diapensiaceae shows that this family retains primitiveness more than the Ericaceae.

Although only a few species of the Diapensiaceae have hitherto been studied embryologically, we can see some pattern different from that of Ericales. The processes of the embryo formation of *Shortia uniflora* do not agree with that of *Diapensia lapponica* (Veillet-Bartoszewska ex Cr  t   1964) which has mega-archetype V of Sou  ges, but very similar to that of *Clethra alinifolia* (Veillet-Bartoszewska 1960) which corresponds to the mega-archetype IV, though in the latter, the first division of the cell *ca* is definitely longitudinal, while in *Shortia uniflora* it is usually transverse and rarely longitudinal. All the embryo formation of the Ericaceae having been studied up to the present is of the mega-archetype VI (Veillet-Bartoszewska 1957, 1958, 1959, 1960 and 1961). In spite of the different patterns of embryo formation in all the families above mentioned, they have a important common character. In all cases, both *icc* and *iec* are differentiated from the same tier, that is to say from *m* itself or from the cell derived from it. These features in the later formation of the embryo, in the authors mind, are the most significant from the phylogenetic stand points. In spite of all the differences mentioned above, the embryogenical features especially in their later stages suggest that the Diapensiaceae should be placed near the Ericaceae, whether this family may be placed in different order Diapensiales or not.

Literatures

- Copeland, H.F., The development of seeds in certain Ericales. Amer. Jour. Bot. **20**: 513-517 (1933)—Cr  t  , P., L'embryog  nie et son r  le dans les essais de classification phylog  n  tique. Phytomorphology **14**: 70-78 (1964)—Diels, L., Diapensiaceen Studien. Bot. Jahrb. **50** (Suppl.): 304-330 (1914)—Doyle, B.E. and L.M. Goss, Some details of the reproductive structures of *Sarcodes*. Madrono **6**: 1-7 (1941)—Hutchinson, J., The families of flowering plants **1**: 282-296 (1959)—Palser, B.F., Early endosperm development and embryogeny in *Cassiope hypnoides*. Trans. Illinois Acad. Sci. **44**: 51-57 (1951)—Studies of floral morphology in the Ericales. VI. The Diapensiaceae. Bot. Gaz. **124**: 200-219 (1963)—Samuelsson, G., Studien   ber die Entwicklungsgechichte der Bl  ten einiger Bicornes-typen. Svensk Bot. Tidskr. **7**: 95-188 (1913)—Schultze-Motel, W., Engler's Syllabus der Pflanzenfamilien **2**: 379-380 (1964)—Stevens, E., Dioecism in trailing arbutus, with notes on the mor-

phology of the seed. Bull. Torr. Bot. Club. **38**: 531-543 (1911)—Veillet-Bartoszewska, M., *Ericacées. Développement de l'embryon chez le Rhododendron ferrugineum* L. C. R. Acad. Sci. Paris **244**: 1952-1954 (1957)—l.c. *Vaccinium myrtillus* L. **246**: 824-826 (1958)—l.c. *Gaultheria shallon* Pursh. **248**: 720-722 (1959)—l.c. *Corema album* Don **249**: 857-859 (1959)—l.c. *Erica tetralix* L. **250**: 1712-1714 (1960)—l.c. *Ledum palustre* L. **251**: 777-779 (1960)—l.c. *Clethra alnifolia* L. **251**: 2572-2574 (1960)—l.c. *Calluna vulgaris* Salisb. **252**: 1192-1194 (1961).

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イワウメ科 (*Diapensiaceae*) は 5 属ほどからなる小さな科で、おもに東アジアと北アメリカに分布している。ツツジ目 (*Ericales*) の一員とされたり、独立のイワウメ目 (*Diapensiales*) としてあつかわれたりしている。材料がてじかに求めにくいため、今までこの群の形態的な研究は殆んど行なわれていず、系統的位置も確証されていなかった。最近ツツジ目の花部形態を研究している Palser が、この類の多くの種類の花の形態と、胚乳の発達のしかたについて研究し、イワウメ科はツツジ目とは別の独立の目としてあつかうのが適当であろうと結論している。系統関係を明らかにするには、胚の組織の分化のしかたが重要であるが、それについての十分な研究がないので、イワウチワ (*Shortia uniflora*) を材料としての結果をここに報告する。

イワウチワの胚嚢のできかたは、他のイワウメ科と同様普通型である。胚乳形成は cellular type で、第 1 回は横に分裂するが、第 2 回分裂は不規則である。この点は他のイワウメ科の報告と一致する。ツツジ目の胚乳形成では、第 1 回分裂は横であるが、第 2 回もすべて横に分裂し、1 列にならんだ 4 細胞のものが作られる。またイワウメ科にはツツジ科にみられるような胚乳吸収器も存在しない。以上のような点で胚乳の発達のしかたにはイワウメ科とツツジ科とはちがいがあがある。細胞分裂の方向が一定していないこと、吸収器の発達しないことは、イワウメ科の胚乳形成のしかたの方がツツジ科より原始的な特徴を示すものであらうと考えられる。

イワウチワの胚形成は Souèges の mega-archetype IV に相当し、Veillet-Bartoszewska が報告した *Diapensia lapponica* が mega-archetype V であるのと異なる。ツツジ科で今まで調べられているものはすべて mega-archetype VI でこれとも異なる。ツツジ目の中ではリョウブ科の胚形成と一致する。ツツジ目では上のように mega-archetype がいろいろ異なるが、これは Souèges の分類自体が機械的で、系統的な意味があまりないことからくるのであって、あまり意義のあるちがいは認められない。胚形成の上で系統的に大きい意義のあるのは、成熟した胚の各組織がどのように分化してくるかにあって、幼胚期における胚柄の分化にあまり重値をおくことはあやまりだと考えられる。ツツジ目の場合、幼根の組織の分化のしかたからみると、cb 層の上端から幼根の原皮層と原中心柱の起源細胞群が分化する。この点は上記のすべての群に共通であり、胚形成がほとんど同じような分化のしかたで行なわれていることを示している。以上のことからイワウメ科は、ツツジ科に近縁の群で、いくつかの点で異なった性質をもっているが、目を異にするほど系統のちがったものではないといえよう。